



El Colegio de la Frontera Sur

Distribución potencial de los abejorros (Apidae: *Bombus*) de
Mesoamérica frente al cambio climático: implicaciones para su
conservación

Tesis
presentada como requisito parcial para optar al grado de
Maestro en Ciencias en Recursos Naturales y Desarrollo Rural
Con orientación en Agroecología

Por

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hacemos constar que hemos revisado y aprobado la tesis titulada

Distribución potencial de los abejorros (Apidae: *Bombus*) de Mesoamérica frente al cambio climático: implicaciones para su conservación

para obtener el grado de **Maestro en Ciencias en Recursos Naturales y Desarrollo Rural**

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DEDICATORIA Y AGRADECIMIENTOS

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Madre, madre, tú me besas, pero yo te beso más, y el enjambre de mis besos no te deja ni mirar...

Si la abeja se entra al lirio, no se siente su aletear. Cuando escondes a tu hijito ni se le oye respirar...

Los ojitos que me diste me los tengo que gastar en seguirte por los valles, por el cielo y por el mar...

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78 **Resumen**

79 Las actividades antropogénicas han transformado los ambientes naturales y amenazan
80 la biodiversidad del planeta. Distintos factores inciden en esta transformación, de los
81 cuales el cambio climático es una de las amenazas más grandes para la biodiversidad.
82 La evidencia indica que el cambio climático afecta y afectará a los abejorros (*Bombus*)
83 en su distribución en Europa y Norte América. Por lo tanto, se evaluó la distribución
84 potencial actual y futura de las especies de abejorros de Mesoamérica bajo tres distintos
85 escenarios de cambio climático (RCP 4.5, 6.0, 8.5), tres modelos (CCSM4, HadGEM2-
86 AO y MIROC-ESM-CHEM) y áreas naturales protegidas de la región. Los resultados
87 indican que la distribución potencial de las 18 especies de abejorros evaluadas se
88 reducirá, no importando el modelo o escenario aplicado. La evidencia cualitativa indica
89 que esta pérdida se dará en sus límites distribucionales. El análisis realizado en las áreas
90 naturales protegidas indica que estas cubren un pequeño porcentaje de la distribución
91 potencial en la actualidad -14% en promedio- pero en los escenarios de mayor pérdida
92 este porcentaje aumenta -23% en promedio-. Se concluye que todas las especies de
93 abejorros en Mesoamérica tendrán una pérdida en sus áreas potenciales de distribución,
94 aunque las especies raras con distribuciones restringidas serán afectadas en mayor
95 medida por el cambio climático que las especies generalistas de amplia distribución.

96

97 **Palabras clave:** *modelaje de nicho ecológico, maxent, áreas naturales protegidas,*
98 *abejas, escenarios de cambio climático*

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108 **Capítulo 1**

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121 **Introducción**

122 Durante los últimos 500 años, la actividad antropogénica en el planeta ha causado
123 cambios importantes en los ambientes naturales (Dirzo et al. 2014; Ripple et al. 2017).

124 El aumento de temperatura, del nivel y de la acidificación de los océanos; deforestación,
125 cambio del uso del suelo, agricultura, urbanización y cambio climático son algunas
126 causas de la modificación del ambiente (Dirzo et al. 2014; Ripple et al. 2017).

127

128 Esto ha provocado que la biodiversidad a nivel mundial se encuentre amenazada y
129 reducida, perdiendo de 11,000 a 58,000 especies anualmente (Potts et al. 2010;
130 Zalasiewicz et al. 2011; Dirzo et al. 2014). Entre los taxones que se encuentran en declive
131 por estas causas están los polinizadores y en especial, las abejas que son las que
132 polinizan la mayoría de las plantas silvestres y cultivos a nivel mundial (Goulson et al.
133 2008; Potts et al. 2010: 345; IPBES 2016).

134

135 Dentro de los polinizadores de plantas silvestres y cultivos a nivel mundial como las
136 abejas, podemos encontrar a un grupo importante, los abejorros del género *Bombus*
137 (Williams 1998; Velthuis and Doorn 2006; Goulson et al. 2008). La evidencia encontrada
138 en la actualidad indica que las poblaciones de abejorros en Europa y Norte América se
139 encuentran en declive según los criterios de clasificación del estado de conservación de
140 la Lista Roja de la Unión Internacional para la Conservación de la Naturaleza (Colla and
141 Packer 2008; Cameron et al. 2011; Bommarco et al. 2012; Williams and Jepsen 2014).

142

143 Los declives poblacionales de las especies de abejorros a nivel mundial han sido
144 atribuidos a: fragmentación del hábitat, pesticidas, contaminación ambiental, disminución
145 en la diversidad y en la abundancia de recursos alimenticios (plantas), contagio de
146 patógenos, introducción de especies no nativas y cambio climático, siendo estos factores
147 los más estudiados (Goulson 2010; Potts et al. 2010; Cameron et al. 2011; Dirzo et al.
148 2014; Kerr et al. 2015; Martins et al. 2015; Rasmont et al. 2015; IPBES 2016)..

149 **Cambio climático y su relación con el declive de abejorros**

150 El cambio climático es un término que se utiliza para indicar una alteración en el estado
151 del clima que puede ser identificado (por ejemplo, utilizando parámetros estadísticos) en
152 un período determinado (incluyendo su promedio y/o la variabilidad de sus propiedades).
153 Estos cambios persisten usualmente por décadas o más tiempo (National Weather
154 Service 2007; Field et al. 2014).

155

156 Las causas del cambio climático pueden ser tanto por procesos internos naturales o
157 fuerzas externas como ciclos solares, erupciones volcánicas, así como cambios
158 antropogénicos persistentes en la composición de la atmósfera o en el uso del suelo
159 (Field et al. 2014). Los impactos de este cambio usualmente se refieren a efectos en la
160 salud, vida, economía, ecosistemas, sociedades, culturas, servicios e infra estructura así
161 como en la biodiversidad (Field et al. 2014)

162

163 Existe un consenso a nivel mundial que la influencia de las actividades antropogénicas
164 en el clima ha tenido efectos sobre la biodiversidad (por ejemplo cambio en la fenología
165 de plantas, en el tiempo de reproducción de animales y/o en su distribución geográfica)

166 (Buse et al. 1999; Hoffmann and Sgrò 2011). Estos cambios son evidentes en los
167 diferentes ecosistemas alrededor del mundo (Root et al. 2003; IPCC 2014). El cambio
168 climático probablemente es una de las amenazas más importantes para la biodiversidad
169 en las próximas décadas (Root et al. 2003; Davis et al. 2010) y hay evidencia que en
170 otros taxones de insectos como mariposas y libélulas han habido cambios en sus
171 distribuciones relacionados con el cambio climático (Stewart 2012).

172

173 A pesar de que el cambio climático probablemente es una de las amenazas más
174 importantes para la biodiversidad, son pocos los trabajos que se han se han realizado
175 para evaluar sus efectos en los polinizadores como las abejas y en especial, en abejorros
176 (ver: Bommarco et al. 2012; Kerr et al. 2015; Miller-Struttman et al. 2015; Rasmont et al.
177 2015; Pyke et al. 2016).

178

179 Como estudio de caso Pyke et al. (2016) demostraron que las especies de abejorros que
180 evaluaron fallaron en adaptarse al cambio en la fenología de las plantas que visitaban,
181 lo cual era una respuesta de las plantas al cambio de temperatura ocasionado por el
182 cambio climático. Por lo tanto, se redujo la sincronía de las comunidades de abejorros y
183 de flores, lo que también causó una reducción en la abundancia de estos polinizadores.
184 Las razones por las cuales los abejorros no logran adaptarse a cambios rápidos en el
185 clima puede estar asociado a su historia evolutiva de origen Paleártico, a regiones
186 montañosas con climas templados-fríos (Hines 2008; Condamine and Hines 2015; Kerr
187 et al. 2015; Rasmont et al. 2015).

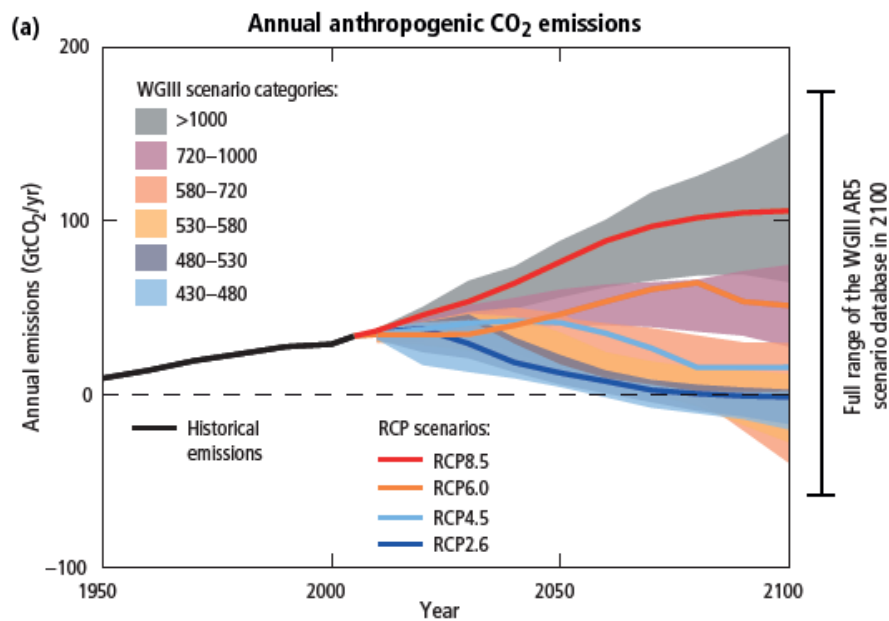
188 Asimismo, se tiene conocimiento que estas especies de abejas tienden a ser más
189 sensibles a otras amenazas (es decir fragmentación del hábitat, pesticidas) cuando se
190 encuentran en sus límites climáticos (Williams and Osborne 2009); estos límites se
191 podrían ver afectados a causa del cambio climático, lo que podría repercutir en las
192 poblaciones de abejorros.

193
194 Hay algunos indicadores de que el cambio climático ha tenido y tendrá un efecto
195 devastador en las poblaciones de abejorros y en su distribución geográfica en Norte
196 América y Europa (Herrera et al. 2014; Kerr et al. 2015), especialmente en los límites de
197 su distribución (Parsons 1990; Corbet et al. 1991; Sexton et al. 2009; Yackulic y Ginsberg
198 2016; Lee-Yaw et al. 2017). Las proyecciones al futuro de la distribución de abejorros de
199 Rasmont et al, (2015) en Europa estiman reducciones moderadas y altas en 34 a 52
200 especies evaluadas para el 2050. Para el año 2100 estiman reducciones en la
201 distribución de 49 a 55 especies de un total de 56 especies evaluadas para ambos
202 períodos.

203 **Escenarios del IPCC**

204 Los escenarios que el Panel Intergubernamental de Cambio Climático (IPCC por sus
205 singlas en inglés) son calculados a partir de diferentes actividades antropogénicas, la
206 última actualización de estos escenarios fue en el año 2014. Estas actividades
207 antropogénicas generan emisiones de gases de efecto invernadero y para la última
208 actualización se tomaron en cuenta las siguientes actividades: tamaño poblacional,
209 actividad económica, estilo de vida, uso de energía, patrones de uso del suelo, tecnología
210 y políticas climáticas.

211 Dependiendo de la intensidad de las actividades antropogénicas se generan las
 212 trayectorias de concentración representativas (Representative concentration pathways
 213 “RCPs” por sus siglas en inglés, Figura 1). Estas proyecciones describen cuatro
 214 escenarios que toman en cuenta gases de efecto invernadero y su concentración
 215 atmosférica, contaminación ambiental y uso del suelo para el siglo XXI. Un escenario
 216 donde hay una rigurosa mitigación de estas causas -RCP2.6-, dos escenarios
 217 intermedios -RCP4.5 y RCP6.0- y un escenario con altas emisiones de gases de efecto
 218 invernadero -RCP8.5- (IPCC 2014)



219

220 Figura 1. Escenarios de cambio climático elaborados por el grupo de trabajo III del
 221 PICC en 2014.

222 *Tomado de Climate Change 2014: Synthesis Report (IPCC 2014)

223 *Modelos de circulación general*

224 Los modelos atmosféricos de circulación general (atmospheric GCMs por sus siglas en
 225 inglés) son modelos matemáticos basados en ecuaciones diferenciales que describen la

226 dinámica y física de la atmósfera, los cuales funcionan como base para simular la
227 circulación global de la atmósfera (Njoku 2014). Cuando a estos modelos se les
228 incorporan otros componentes del clima (e.g. ciclo del carbón, capas de hielo) estos
229 pueden tener aplicaciones en el campo del cambio climático y sus predicciones,
230 típicamente para períodos entre 10 y 1,000 años (Njoku 2014).

231
232 Por lo tanto, cada modelo tiene diferentes supuestos y tratan de representar la
233 incertidumbre del clima basado en observaciones limitadas, un entendimiento imperfecto
234 del sistema, y recursos computacionales finitos (Knutti et al. 2013). Todos estos
235 supuestos hacen que estos modelos sean útiles para explorar la incertidumbre generada
236 por los distintos factores que interactúan en el cálculo del cambio climático, lo cual los
237 convierte en herramientas importantes e irremplazables que permiten proyectar el
238 cambio del clima al futuro (Knutti et al. 2013).

239
240 En el sitio de Worldclim hay 19 modelos para el 2050 y 2070, aunque no todos tienen
241 proyecciones para cada escenario (http://www.worldclim.org/cmip5_30s) (Cuadro 1). En
242 este estudio utilizamos tres modelos diferentes basados en el reporte del PICC (2014) y
243 el sitio de Infraestructura y Red Climática (Infrastructure & Climate Network) “Escogiendo
244 un GCM para proyectos pilotos y de investigación”, así como la disponibilidad de estos
245 modelos para los escenarios escogidos en el sitio de Worldclim los cuales fueron: 1)
246 **CCSM4**, 2) **HADGEM2-AO** y 3) **MIROC-ESM-CHEM** en negrita en el cuadro 1.

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Cuadro 1. Modelos disponibles en Worldclim para las distintas trayectorias de

250

concentración representativas

GCM	RCP26	RCP45	RCP60	RCP85
ACCESS1-0		X		X
BCC-CSM1-1	X	X	X	X
CCSM4	X	X	X	X
CESM1-CAM5-1-FV2		X		
CNRM-CM5	X	X		X
GFDL-CM3	X	X		X
GFDL-ESM2G	X	X	X	
GISS-E2-R	X	X	X	X
HadGEM2-AO	X	X	X	X
HadGEM2-CC		X		X
HadGEM2-ES	X	X	X	X
INMCM4		X		X
IPSL-CM5A-LR	X	X	X	X
MIROC-ESM-CHEM	X	X	X	X
MIROC-ESM	X	X	X	X
MIROC5	X	X	X	X
MPI-ESM-LR	X	X		X
MRI-CGCM3	X	X	X	X
NorESM1-M	X	X	X	X

251

*Modificado del sitio de Worldclim (2018)

252 *CCSM4 – HADGEM2-AO – MIROC-ESM-CHEM*

253 El modelo CCSM (“Community Climate System Model”) es un modelo de circulación
254 general conformado por diferentes componentes como lo son: atmósfera, tierra, océano
255 y hielo marino. Este modelo toma en cuenta la información y flujos de sus varios
256 componentes para hacer proyecciones en el pasado así como para el futuro (Gent et al.
257 2011).

258

259 La familia de modelos de circulación general HadGEM2 (“Hadley Global Environment
260 Model 2”) está conformado por distintos componentes los cuales son: atmósfera, océano,
261 componentes del hielo marino, con o sin extensión vertical en el modelo atmosférico que
262 incluye a la estratósfera, componentes de la tierra que incluyen ciclos de carbono
263 terrestre y marino, así como composición química de la atmósfera (Martin et al. 2011).

264 La configuración HADGEM2-AO incluye diferentes procesos a diferencia de otros
265 modelos dentro de la misma familia. Este modelo incluye procesos en la tropósfera,
266 superficie terrestre, hidrología, aerosoles y hielo marino (Martin et al. 2011).

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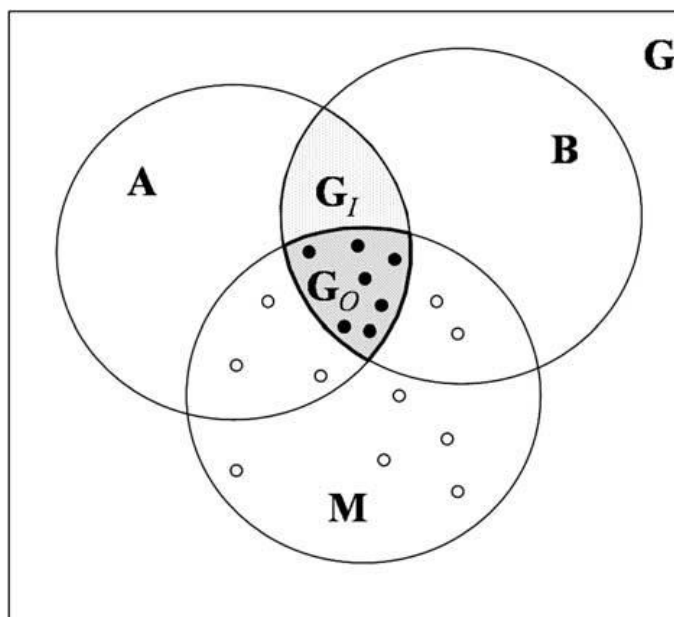
268 El modelo de circulación general MIROC (“Model for Interdisciplinary Research on
269 Climate”) está compuesto por componentes como son: aerosoles, océano y hielo marino,
270 superficie terrestre y sus interacciones (Watanabe et al. 2011). El modelo MIROC-ESM-
271 CHEM además agrega a estos componentes aspectos químicos de la atmósfera,
272 nutrientes de phytoplankton y zooplankton dentro del componente oceánico así como
273 vegetación dinámica terrestre (Watanabe et al. 2011).

274 **Presentación del artículo de tesis**

275 A raíz del trabajo que hemos realizado el equipo de Abejas de Ecosur con abejorros en
276 distintos campos de la biología, mi inquietud sobre cómo el cambio climático pudiera
277 afectar a las especies de abejorros de México y Centro América y la bibliografía
278 presentada en el capítulo introductorio, la pregunta de mi investigación fue la siguiente:
279 ¿Se reducirá la distribución potencial futura de las especies de abejorros (*Bombus*) en
280 Mesoamérica por el cambio climático, tanto en sus límites geográficos como en áreas
281 naturales protegidas? Para poder responder esta pregunta utilicé el modelaje de nicho
282 ecológico bajo la teoría de nicho de Grinnel. Este marco teórico define al nicho ecológico
283 de una especie basado en variables que no son afectadas por la especie (llamadas
284 scenopoéticas, i.e. temperatura humedad) y condiciones ambientales a escalas
285 geográficas considerables, lo cual es necesario para comprender las propiedades
286 ecológicas y geográficas de una especie (Soberón 2007).

287

288 Asimismo, para poder estimar y comprender el nicho grinneliano, Soberón y Peterson
289 (2005) sintetizaron esta información bajo un diagrama de Venn, llamado diagrama de
290 BAM (relación entre lo biótico, abiótico y la dispersión “Biotic-Abiotic-Movility”) (Soberón
291 2010).



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Figura 2. Diagrama de BAM

*Tomado de Soberón 2010

En este diagrama, la región **G** representa la región geográfica entera a considerar. La región **A** es el área donde las condiciones scenopoéticas son favorables para la especie. Esta es una región potencial, probablemente no ocupada en su totalidad por la especie. La región **B** es el área en donde las condiciones bióticas son idóneas para la especie. La región **M** es el área en la cual la especie ha podido alcanzar dada su capacidad de dispersión y un tiempo determinado. La intersección entre **A**, **B** y **M** equivale a **G_O**, la cual representa el área actual de distribución de las especies. La intersección entre **A** y **B**, diferente a **G_O**, equivale a **G_I**, la cual representa la región que potencialmente puede ser invadible dado que ambas condiciones (A y B) son idóneas, pero que la especie no ha podido alcanzar durante un tiempo determinado (Soberón 2010).

De las tres regiones a considerar para los modelos de nicho ecológico (A, B y M), los datos que se tienen para construir el nichos ecológico de una especie usualmente

309 provienen de A -variables bioclimáticas como Bioclim- (Hijmans et al. 2005) y de M, la
310 cual es la región que definimos basado en el conocimiento de la especie y los lugares a
311 los cuales ha tenido acceso durante cierto tiempo. En el caso de B, es muy difícil de tener
312 datos ya que en general, para estimar este parámetro se necesita un conjunto de datos
313 en escalas espaciales gruesas, donde se puedan verificar las diferentes interacciones
314 que ocurren entre las especies en esa escala y que, probablemente, puedan ser
315 diferentes en toda la región de estudio (Soberón 2010).

316

317 Bajo este esquema operacional, mi objetivo fue evaluar la distribución potencial de las
318 especies de abejorros (*Bombus*) de Mesoamérica frente al cambio climático. Asimismo,
319 basado en los análisis que realicé, comparé la distribución potencial actual con la
320 distribución potencial futura de estas especies en su rango distribucional, así como en
321 áreas naturales protegidas. Mi predicción fue la siguiente: si la distribución potencial de
322 las especies de abejorros (*Bombus*) de Mesoamérica es reducida por efectos del cambio
323 climático, entonces esta reducción será evidente en la distribución potencial futura de las
324 especies de abejorros de Mesoamérica y ocurrirá en los límites geográficos de las
325 especies.

326

327 Asimismo, se evaluó el porcentaje de cobertura de áreas naturales protegidas en la
328 distribución potencial actual y futura de las especies de abejorros, ya que estas áreas
329 juegan un papel importante en la conservación de especies y en el futuro tendrán un rol
330 importante en la conservación de la biodiversidad, incluidas las abejas y los abejorros.

331 Por lo tanto, el siguiente capítulo es el artículo científico que se realizó para responder la
332 pregunta de investigación y alcanzar el objetivo propuesta para la maestría. Finalizado
333 el capítulo dos, se describen las conclusiones que fueron derivadas de este estudio.

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Capítulo 2

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370 **Potential distribution of bumble bees (*Apidae: Bombus*) in Mesoamerica based on different climate**
371 **change scenarios: conservation implications**

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395 **Abstract**

396 Mesoamerica's wide range of biodiversity arise from the region's intricate, biogeographical history.
397 Bumble bee species found in Mesoamerica are ecologically different from European and North American
398 species due to environmental and seasonal constraints that are unique to the region. Our study aimed
399 to estimate the future impact that climate change will have on 18 Mesoamerican bumble bee species.
400 To do so we used ecological niche modelling and current climate and future climate change scenarios
401 (RCP 4.5, 6.0 & 8.5) and models (CCSM4, HadGEM2-AO, MIROC-ESM-CHEM). We calibrated and
402 projected the models in Maxent using climate records from 1940-2017 and environmental variables
403 from 1950-2000. Our estimations indicate that all 18 bumble bee species will experience a reduction in
404 their potential distribution and environmental suitability due to climate change, regardless of the model
405 and scenario applied. It seems that the reduction in their geographical range will be more evident at the
406 limits. Protected natural areas cover a small proportion of each species' current potential distribution
407 (14% on average), and this proportion would increase (23% on average) in the worst climate change
408 scenarios. We conclude that climate change will be a major threat to these Mesoamerican pollinators,
409 especially the rare species, by substantially reducing their potential distribution ranges and suitability.
410 Protected natural areas could help protect bumble bee species, but the proportion of current and future
411 potential distribution that lies in these areas is low. Effective landscape management that includes the
412 restoration of pine-oak forests habitats and native flowering plants could benefit these pollinators.

413 Key words: Maxent, protected natural areas, ecological niche modelling, pollinators, representative
414 concentration pathways

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423 1. Introduction

424 Mesoamerica host an exceptionally wide range of biodiversity due to the intricate biogeographical
425 history, habitats, geomorphic processes, and climate dynamics that have shaped the region's flora and
426 fauna (Gutiérrez-García and Vázquez-Domínguez, 2012; Halffter, 1987; Morrone et al., 1999). The
427 complexity of this region makes it a biodiversity hotspot (Myers et al., 2000), and particularly a place in
428 the world where the insects that live at high, mountainous elevations (*e.g.* bumble bees) are
429 characteristically different from the insect fauna found in the contiguous lowlands (Halffter, 1987).
430 These entomofaunas' dissimilarities are attributed to their different biogeographic history (*e.g.* Neartic
431 and Neotropical influence), insularity and refugee effects on mountains separated by low-land valleys,
432 and major biogeographical barriers such as the Isthmus of Tehuantepec and the Nicaraguan Depression
433 (Duennes et al., 2017; Halffter, 1987; Koch et al., 2018).

434 Bumble bees (*Bombus*) species are high mountain insects that are more common and diverse in artic,
435 subartic, and boreal regions of the world and are considered an important group of pollinators (Goulson,
436 2009; Hines, 2008; Velthuis & Doorn, 2006). South of the United States these bees are most commonly
437 recorded in temperate zones or in highland areas, although some species occur in lowlands (Hines,
438 2008; Labougle, 1990). The bumble bee species found in Mesoamerica are ecologically different from
439 European and North American species (*e.g.* behavior, activity throughout the year), due to
440 environmental and seasonal constraints that are unique to this region (Labougle, 1990; Plowright and
441 Laverty, 1984). These region-specific, environmental constraints have also played an important role in
442 the isolation of certain populations and in speciation processes, as was recently documented for two
443 bumble bees species in Mesoamerica: *B. ephippiatus* and *B. huntii* (Duennes et al., 2017; Koch et al.,
444 2018). These regional particularities offer a unique opportunity for studying different aspects of the
445 ecology and distribution of bumble bee species in the region. Considering that global changes are
446 causing and will continue to cause population and species declines worldwide, this study seeks to shed
447 light on the future distribution patterns of bumble bees across the region. These findings will provide
448 information that will be useful for designing plans that support conservation of these important
449 pollinators.

450 Different global changes are causing landscape transformation and loss of species. Rising sea levels,
451 increasing ocean temperatures and acidification, deforestation, land use change, agriculture,
452 urbanization, and climate change are the major causes of the aforementioned phenomena (Dirzo et al.,
453 2014; Ripple et al., 2017). These changes significantly threaten biodiversity worldwide, and it is

454 estimated that between 11,000 to 58,000 species are lost annually (Dirzo et al., 2014; Potts et al., 2010;
455 Zalasiewicz, Williams, Haywood, & Ellis, 2011). Human activities are the primary force behind these
456 changes, and of all these anthropogenic activities climate change is considered to be the single most
457 important threat to biodiversity in the coming decades (Davis et al., 2010; Root et al., 2003),
458 Climate change is driven by the Earth's internal natural processes or by external forces (e.g. volcanic
459 eruptions, solar cycles), and persistent anthropogenic changes in the atmosphere's composition and
460 land-use change (IPCC, 2018). There is a worldwide consensus that anthropogenic activities have
461 significantly influenced climate patterns by increasing greenhouse gas emissions, especially carbon
462 dioxide (CO₂), methane (CH₄), and nitrous oxide (N₂O) since 1750 (IPBES, 2016; IPCC, 2018). This
463 concentration of gases has caused global land and ocean surface temperatures to increase an average of
464 0.85°C between 1800 and 2012 (IPCC, 2014). The effects of climate change have been documented in
465 different biological groups with a broad range of consequences that include modifications in the
466 phenology and sexual reproduction of plants and animals (Bartomeus et al., 2011; Burkle et al., 2013;
467 Hoffmann and Sgrò, 2011), and changes in species' geographic distributions (IPBES, 2016; Parmesan,
468 2006; Stewart, 2012). These changes are evident on a global scale and in a variety of ecosystems (IPCC,
469 2014; Parmesan, 2006; Root et al., 2003; Walther et al., 2002).

470 Pollinators, and particularly bees, are among the taxa whose declining population size has been
471 documented, and this loss is of significant concern because of their role in pollinating wildflowers and
472 crops around the globe (IPBES, 2016; Velthuis and Doorn, 2006). Nevertheless, little research has been
473 conducted on how climate change has affected pollinators such as bees and bumble bees and how it
474 may affect them in the future. The possible consequences that climate change may impose on
475 pollinators can be seen in the literature. These impacts range from changes in distribution patterns, the
476 disruption and mismatch of pollination services, the loss of species and populations, and an increase in
477 diseases related to pollinators (Imbach et al., 2017; IPBES, 2016; Le Conte and Navajas, 2008; Martins et
478 al., 2015; Miller-Struttman et al., 2015; Pyke et al., 2016).

479 Published information on how climate change could affect bees is scarce for tropical areas (Imbach et
480 al., 2017; Le Conte and Navajas, 2008). One of these studies found that if two different climate change
481 scenarios were to occur, bee richness in the tropical region of Latin America would be reduced by 65%.
482 This decline could potentially disrupt pollination services for coffee production and would especially
483 affect bee populations in low montane areas (Imbach et al., 2017). These results were tested with
484 stingless bees and honey bees, but no analysis has been conducted with regard to bumble bees. The

485 results published by Imbach et al. (2017) suggest future scenarios in which several bee species would
486 remain unaffected by climate change; however, they also indicate that the majority of species will be
487 negatively impacted and that these impacts will vary depending on the species and the pollination
488 services they provide.

489 Evidence from recent years indicates that populations of bumble bees across Europe and North America
490 are decreasing in size, and several species are at different levels of extinction threat based on the Red
491 List criteria of the International Union of Conservation (IUCN) (Bommarco et al., 2012; Cameron et al.,
492 2011; Williams and Jepsen, 2014). Climate change is one of the main factors associated with this decline
493 as well as shifts in community composition (Kerr et al., 2015; Miller-Struttman et al., 2015; Rasmont et
494 al., 2015). Climate change will have a devastating effect on bumble bee populations size and
495 geographical distributions in North America and Europe (Herrera et al., 2014; Kerr et al., 2015; Sirois-
496 Delisle and Kerr, 2018), especially in terms of the limits of their distribution (Corbet et al., 1991; Parsons,
497 1990).

498 Future distribution projections for bumble bees made by Rasmont et al. (2015) in Europe are pessimistic
499 about how climate change will affect the distribution of several species given that their results indicate
500 that these species will experience a moderate to high decline in their distribution. Kerr et al. (2015)
501 showed that bumble bees from Europe and North America respond to range expansion in ways that are
502 the opposite of how other terrestrial assemblages respond. Specifically, they have rapid range loss in the
503 southern part of their distribution and fail to expand in the northern part of their distribution. The
504 probable cause of this behavior has been linked to their evolutionary history dating back to their
505 Palearctic origin in mountainous regions with temperate-cold climates (Kerr et al., 2015; Rasmont et al.,
506 2015). Likewise, it is known that these bees tend to be more sensitive to other threats (e.g. habitat
507 fragmentation, pesticides) when they dwell in their climatic limits (Williams & Osborne, 2009), the
508 impacts of which could become even more severe because of climate change.

509 Our study builds on previous studies of how climate change has and will affect North American and
510 European bumble bees and remedies the lack of studies that relate bumble bees and climate change in
511 Mesoamerica. In order to understand how climate change may affect bumble bees in this region we
512 applied a purely niche-based model that first estimates the suitability of a species based on the present
513 environmental data. This model then became the basic input for projecting future conditions given
514 different climate change scenarios and, based on these results, estimating the areas that could be
515 suitable/unsuitable for the species (Anderson, 2013; Rasmont et al., 2015).

516 The objective of this study was to determine the current potential distribution (**CPD**) and future
517 potential distribution (**FPD**) of 18 bumble bee species in Mesoamerica based on contemporary climate
518 and climate change representative concentration pathways -RCP 4.5, 6.0 & 8.5- (IPCC, 2014) and global
519 circulation models -GCM CCSM4, HadGEM2-AO, MIROC-ESM-CHEM- using ecological niche modelling.
520 We predict that bumble bee species from Mesoamerica will have FPDs reduced in relation to their CPDs
521 and a decrease in their environmental suitability based on climate change scenarios and models. We
522 hypothesize that rare species i.e. those with smaller range distributions, will have a stronger reduction in
523 their CPD than common species i.e. those with larger range distributions (Gaston, 1997). Additionally,
524 we tested the hypothesis that the limits of the species' geographical range will be the main areas to be
525 lost. Finally, we estimated how much of the CPD and FPD of bumble bee species is covered by protected
526 natural areas.

527 **2. Methods**

528 To estimate the CPD and FPD of 18 bumble bee species we applied an ecological niche modelling
529 approach based on Grinnellian niche theory and the BAM conceptual framework (Soberón & Townsend
530 Peterson, 2005). For each species we used a set of abiotic environmental conditions (**A**) as well as a
531 calibration area (**M**). We estimated **A** for each species based on the environmental conditions present in
532 the species occurrence data. To define **M**, we considered the geographic location of the species records,
533 the knowledge of the geographic distribution of each species and expert knowledge. We used different
534 representative concentration pathways (**RCPs**) (IPCC, 2014) and models to transfer the estimated
535 potential distribution outside **M**, in México and Central America which is defined as **G'** in the BAM
536 conceptual framework.

537 *2.1 Species records*

538 We used georeferenced records dating from 1940 to 2018 for all bumble bee species. We gathered
539 occurrence data from different data sources concentrated in the database of bees in Mesoamerica built
540 and stored by El Colegio de la Frontera Sur -ECOSUR-
541 (<http://www.ecosur.mx/sitios/beesofmesoamerica>). Prior to modelling, each species' records were
542 taxonomically classified by expert taxonomists from Ecosur, Philippe Sagot and Jorge Mérida using the
543 taxonomic key for bumble bee species of Mesoamerica proposed by Labougle (1990). Each record was
544 checked to ensure its geographical accuracy. Two bumble bee species in our study area have a broader
545 distribution beyond Mesoamerica (*B. pensylvanicus* and *B. variabilis*), extending to the United States and

546 Canada. To obtain records for both species we used the Global Biodiversity Information Facility (GBIF)
547 database. We discarded records that were difficult to geo-reference for the following reasons: (1)
548 labeling errors or inconsistency in the labeling (e.g. Mexico as a locality), (2) being limited to human
549 observations, or (3) lacking information on collection repository in GBIF. We considered the Mexican
550 population of *B. huntii* as ecologically and genetically distinct from the populations in United States and
551 Canada (Koch et al., 2018).

552 To reduce sampling bias due to oversampled areas we calibrated the CPD for each species using only
553 one occurrence filtered to one-per-cell spatial resolution of the environmental layers used (30 arc
554 seconds) (Romero-Alvarez et al., 2017). Using the full data set we generated a sampling effort raster
555 map to account for differences in sampling effort (Hatfield et al., 2015). This map showed the areas that
556 were better surveyed, which in turn helped us to identify possible caveats in our models and improve
557 the interpretation of results (Lobo, 2008) (Fig. 1).

558 *2.2 Environmental variables*

559 We used the 19 current (1960-1990) and future (2050, and 2070) bioclimatic environmental layers from
560 Worldclim (<http://www.worldclim.org/version1>) at the spatial resolution of 30 arc-sec (Hijmans et al.,
561 2005) (Supplementary material Table. A1). For FPDs we RCPs (4.5, 6.0 & 8.5) and global circulation
562 models (**GCMs**) (CCSM4, HadGEM2-AO, MIROC-ESM-CHEM). The RCPs represent different climate
563 change projections that take into account the atmospheric concentration of greenhouse gases as well
564 as, pollution and land-use change during the twenty-first century (IPCC, 2014). There are two
565 intermediate greenhouse emission scenario (RCP 4.5 & 6.0) and a high emission scenario (RCP 8.5). For
566 each scenario there are different GCMs (19 on Worldclim) that take into account different parameters.
567 These models evolve, and are considered irreplaceable tools for projecting future climate changes
568 (Knutti et al., 2013). Using different models can capture the variability that is intrinsic to climate models,
569 thus, using several models can help capture such variability on the species FPD (Fig. 2). We used the
570 abovementioned RCPs and GCMs based on the IPCC Fifth Assessment Report (2014), the expertise of the
571 Infrastructure & Climate Network “Choosing GCM’s for pilot and research projects”, and the availability
572 of these three models for each of the chosen climate change scenarios on the Worldclim site.

573 The environmental variables chosen to model the potential distribution of each species were selected
574 using a framework that included a number of steps and criteria: (1) we generated a model with all the
575 19 bioclimatic variables, (2) conducted a correlation analysis of variables with a cut-off value ($r > + 0.80$)

576 (Jarnevich and Reynolds, 2011), and (3) used the model feedback together with the correlation analysis
577 to decide which variables were relevant for providing a possible biological explanation for the species
578 final models.

579 *2.3 Ecological niche models and potential distribution areas*

580 We used the algorithm of Maximum Entropy -Maxent 3.4.1 (Phillips et al., 2017) for the species
581 distribution modelling. Maxent is a machine learning algorithm that estimates a species' response based
582 on environmental variables. It characterizes the background environment available in the modelling
583 area according to presence-only records (Phillips et al., 2017). For tuning and other analyses, we used
584 different packages within the software R version 3.5.1 (<https://www.r-project.org/>). To choose the
585 optimal settings (e.g. features) for each model in Maxent we ran preliminary models in "Wallace"
586 package (Kass et al., 2018), which is an open-source GUI application. This package uses the "ENMeval"
587 package (Muscarella et al., 2014) as well as Maxent to find optimal models based on the optimal settings
588 as decided by the Akaike's Information Criterion (**AICc**) corrected for small sample size (Romero-Alvarez
589 et al., 2017).

590 For the final models, the settings used in Maxent for each species were the following: twenty replicates
591 for each species using the optimal settings with cross-validation method, and we chose a maximum
592 number of background points of 50 000 rather than the default value of 10 000 to better characterize
593 the background. We did not apply clamping, and we chose to extrapolate. These settings allowed us to
594 tune our models and better characterize them, which is critical given that we are working with model
595 transfer to a different time/area (Muscarella et al., 2014). We also present the values of the area under
596 the curve (AUC), although it has been noted that AUC values are misleading and should be treated with
597 caution (Lobo et al., 2008). To complement these models with a measure that can quantify the
598 environmental similarity between the **M** and **G'** as well as areas where strict extrapolation occurs, we
599 used Multivariate Environmental Similarity Surface (**MESS**) (Elith et al., 2010) (Supplementary Material
600 Fig. A1).

601 Next, the results of the Maxent models were converted from continuous to binary data (defined by a
602 threshold) to better understand the results. The method used to define a threshold was based on
603 Jiménez-Valverde (2014), in which the best criteria to apply a threshold is the one in which Sensitivity =
604 Specificity, as opposed to other methods that have been used like Minimum Training Presence, 10
605 Percentile Training Presence, or Maximizing the sum of sensitivity and specificity (Jiménez-Valverde,

606 2014; Liu et al., 2016) (Supplementary material Table. A2). Area estimates (in hectares) were made using
607 Behrmann cylindrical equal area projection (Snyder, 1987). We then intersected the CPD with the FPD
608 areas to obtain areas of stable potential distribution in the future (**SPD**). This result left us with three
609 areas to visualize in the geographic space that we defined with colors: red for lost areas, yellow for
610 stable areas and green for novel areas (Fig. 2).

611 Based on these estimates, we calculated the difference between CPD and SPD to assess the loss in FPD
612 for the year 2050, and 2070 (Table. 3 and Table. 4). We also focused these calculations on protected
613 natural areas to assess their future relevance for bumble bee conservation (Fig. 3).

614 *2.4 Correlation analyses and environmental suitability change*

615 To assess the relationship between the size of bumble bees CPDs and the mean change in FPDs by
616 climate change we performed a Pearson correlation coefficient analysis using RCPs and GCMs for 2050
617 and 2070. Additionally, we estimated the environmental suitability values in all species records between
618 CPD and FPDs for each RCP and GCM.

619 For the correlation analysis we first normalized each species' CPD and FPD separately with the following
620 formula:

$$621 \left(\frac{X - \bar{X}}{\sigma} \right)$$

622 where **X** represents the CPD or FPD in ha of a species, \bar{X} represents the mean of all the species' CPD or
623 FPD in ha and σ represents the standard deviation of all species' CPD or FPD. For FPDs we separated the
624 correlation analysis into two timelines: 2050 RCP scenarios/models (Fig. 4) and 2070 RCP
625 scenarios/models (Supplementary material Fig. A.2). To conduct the environmental suitability analysis,
626 we obtained the corresponding suitability value for the CPD and FPD of each RCP and GCM for each
627 occurrence point per species. Then, we calculated the difference between the CPD and FPD values. Next,
628 we calculated how much suitability was gained or lost for each species per model and scenario. Finally,
629 we conducted a box-plot analysis that included the quartiles of the RCP 4.5 models and the median of
630 the three models and scenarios for 2050 (Fig. 5) and 2070 (Supplementary material Fig. A.3).

631

632

633 **3. Results**

634 *3.1 Sampling effort, current potential distribution and future potential distribution*

635 The sampling effort, which is represented by the availability of records of Mexican and Central American
636 bumble bee species, varies among regions. Figure 1 shows that portions of the following mountain
637 ranges are well surveyed in Mexico: The Sierra Madre Oriental, Trans-Mexican Volcanic Belt, Sierra
638 Madre del Sur, Sierra Madre de Chiapas. In Central America these well surveyed areas include the
639 Guatemalan highlands and Costa Rica Talamanca montane forests. The Sierra Madre Occidental of
640 Mexico is less well surveyed, and the sampling effort decreases in Baja California, Yucatan Peninsula, El
641 Salvador, Honduras, Nicaragua and Panama.

642 According to the results of ecological niche modelling, the estimated CPD of bumble bee species ranges
643 from 561,298 ha for *B. xelajuensis* up to 125,530,939 ha for *B. pensylvanicus*. Based on this finding we
644 divided the species in two groups. The first group, consisting of rare species with CPDs less than 15
645 000.000 ha includes *B. digressus*, *B. huntii*, *B. macgregori*, *B. nigrodorsalis*, *B. trinominatus*, *B. wilmattae*,
646 and *B. xelajuensis*. A second group made up of species that are more common in highlands, and low-
647 land species with broader CPD includes *B. brachycephalus*, *B. ephippiatus*, *B. haueri*, *B. medius*, *B.*
648 *mexicanus*, *B. pensylvanicus*, *B. pullatus*, *B. steindachneri*, *B. variabilis*, and *B. weisi*. All RCPs and GCMs
649 show that there will be a decrease in bumble bees' FPDs ranging from a minimum of 7% for *B.*
650 *steindachneri* for RCP 6.0 up to 100% for *B. xelajuensis* in RCP 4.5.

651 *3.2 Geographic edges and protected natural areas*

652 The intersection of CPDs with FPDs allowed us to evaluate the lost area (red areas) and the stable areas
653 (yellow areas). The lost areas are usually at the margins of the stable areas; this is consistent for all of
654 the 18 bumble bee species. The intersection of CPD and SPD was also carried out for protected natural
655 areas for different RCPs scenarios and GCMs. Figure 3 provides an estimate of the CPD and SPD areas
656 within protected natural areas. The CPD within protected natural areas is 14% on average with a range
657 from 7% to 16% for almost all species except for *B. digressus*, which is 52%. The minimum average
658 estimate of proportion of SPDs within protected natural areas is 12% with a range from 0% to 16%,
659 except, again, for *B. digressus* with 52%. The maximum average for all SPD estimates is 23% with a
660 range from 8% to 48%; *B. digressus* being the exception with 68%.

661

662 3.3 Correlation analyses and environmental suitability change for bumble bee species

663 The results obtained by the correlation analyses showed a positive correlation between the size of
664 bumble bees' CPD with the mean change of FPD for the year 2050 ($n = 18$, $r = .70$, $p < 0.01$), and 2070 ($n =$
665 18 , $r = .69$, $p < 0.01$). The correlation is stronger for 2050 ($n = 17$, $r = .94$, $p < 0.01$), and 2070 ($n = 17$, $r = .92$,
666 $p < 0.01$) if we do not take into account *B. pensylvanicus*, which is a species that has a broader
667 distribution than all of the other species and inhabits a wide range of habitats extending into eastern
668 Canada and the United States (Hatfield et al., 2015). Both correlation analyses are summarized in Figure
669 4, and Supplementary material Figure A.2. Overall, species that are rare (have smaller CPDs) such as *B.*
670 *digressus*, *B. huntii*, *B. macgregori*, *B. nigrodorsalis*, *B. trinominatus*, and *B. xelajuensis* will be more
671 affected by climate change on average compared to low-land species or species with broad potential
672 distributions that are more common like *B. brachycephalus*, *B. ephippiatus*, *B. medius*, *B. mexicanus*, *B.*
673 *steindachneri*, and *B. variabilis*.

674 The environmental suitability analysis for bumble bee species showed that, in general, all species will
675 have a reduction in their environmental suitability for all RCPs and GCMs. Rare species tended to
676 perform worse than common species. Comparing the median of all GCMs for the year 2050, the RCP 4.5
677 models tended to reduce suitability more than RCP 6.0, and the RCP 8.5 models, which is likely to have
678 the greatest effect of the three RCPs. For the year 2070 the RCP 4.5 models tended to reduce suitability
679 less than the RCP 6.0 and RCP 8.5 models respectively.

680 4. Discussion

681 4.1 Sampling effort biases, current and future potential distributions of bumble bees in Mesoamerica

682 We believe that we had adequate sampling effort in areas of the region we analyzed, and we feel that
683 our models appear to transfer fairly well based on MESS analyses. Nonetheless, we are still unsure of
684 whether the CPD is transferable in space and time for certain bumble bee species. Precautions on the
685 forecast should be considered for *B. medius*, *B. mexicanus*, *B. pensylvanicus*, and *B. pullatus*. *Bombus*
686 *pensylvanicus* has a broad distribution in northern Mexico; however, there are still places in the Sierra
687 Madre Occidental and other regions in the northern states of Mexico that have not been properly
688 surveyed. *Bombus medius*, *B. mexicanus*, and *B. pullatus*, are species distributed in low-land regions of
689 Mesoamerica where sampling has been limited and our forecasts for these species and *B. pensylvanicus*
690 should be treated with caution.

691 Nevertheless, based on the different RCP scenarios, models, and the analyses conducted, we found
692 several general patterns in bumble bee FPDs in Mesoamerica. All species analyzed showed a decrease in
693 their FPD compared to their CPD. Although the GCMs tended to vary between them and among RCPs,
694 especially MIROC-ESM-CHEM which tended to be more extreme, they all showed a decrease in the
695 species' FPD. Based on the correlation analyses, rare species, with smaller CPDs would be more severely
696 affected than common species with broader CPDs. Additionally, there would be a reduction in their
697 environmental suitability. These results are consistent with the estimated loss of potential distribution
698 for other bees and bumble bee species worldwide (Giannini et al., 2012; IPBES, 2016; Kerr et al., 2015;
699 Martins et al., 2015; Rasmont et al., 2015; Sirois-Delisle and Kerr, 2018).

700 Consistent with other studies of Apoidea (Giannini et al., 2012; Martins et al., 2015; Williams, 1988), we
701 found area reductions of bumble bees' FPD at the edges of their CPD in Mesoamerica, whereas areas
702 closer to the center of their distribution persisted. The hypothesis that areas at the geographic limits of
703 a species' distribution will be the main areas that are lost and that the center of its distribution will
704 persist is supported by published, empirical evidence (Brown, 1984), yet there is still a debate on why
705 this occurs (Gaston, 2003; Martínez-Meyer, Díaz-Porrás, Peterson, & Yáñez-Arenas, 2013; Soberón,
706 Peterson, & Osorio-Olvera, 2018). Although our study only explores this idea in the geographical space,
707 important questions also remain to be addressed in the environmental space that, if complemented
708 with demographic studies, could unveil the pattern that we explored in this study.

709 It is important to mention that all species could colonize new areas that are not present in their CPD. We
710 did not take these areas into account for the analyses because we still need more information on the
711 dispersion patterns of bumble bee species in Mesoamerica. We believe that our study lays the
712 groundwork for future analyses that should consider dispersion and demographic information, just as
713 Anderson (2013) proposed. Nevertheless, it is relevant to note that in Europe, regardless of a species'
714 dispersal abilities, climate change will decrease climatic suitable areas and no extra suitable regions will
715 emerge for 30% of bumble bee species. If full dispersal assumptions are taken to be true, only three or
716 four species there could expand their ranges, while another 25 species would be at high climatic risk
717 (Rasmont et al., 2015). In Canada and the United States, even when the dispersal abilities of bumble bee
718 species are taken into account, about half of the modeled species' ranges are expected to decline
719 (Sirois-Delisle and Kerr, 2018).

720

721 4.2 The role of protected natural areas for bumble bees under climate change

722 Protected terrestrial areas act as core units for conservation (Chape et al., 2005), and they can help to
723 protect disconnected areas of bumble bees' FPDs (Martins et al., 2015). However, the geographic space
724 designated for many protected areas around the world was not chosen for species protection, but
725 rather because they met other criteria (i.e. scenic beauty, unproductive landscapes); and in our study
726 region many protected areas are small, disconnected or highly threatened (Miller et al., 2001; Monteiro
727 et al., 2018; Pressey et al., 2002). Our results showed that protected natural areas in Mesoamerica cover
728 a small fraction of bumble bee species' CPD and FPD. An exception is *B. digressus* in which more than
729 half of its CPD is included within protected natural areas, which are mainly in Costa Rica.

730 The increase in the proportion of bumble bee species' FPD within protected natural areas is a
731 consequence of a larger proportion of area lost in FPD elsewhere. A greater FPD in protected natural
732 areas does not necessarily indicate that bumble bee species in these areas will be protected from
733 climate change effects, especially since coverage is limited. Factors other than climate change will also
734 contribute to area loss in FPD outside protected natural areas, such as land-use change (i.e. agriculture
735 expansion) which also comes accompanied by other threats for bees like pesticides, landscape
736 fragmentation, and loss of forest habitat near protected areas (DeFries et al., 2005; Rafferty, 2017). Even
737 if some bees are resilient to fragmentation in the Neotropics (Jaffé et al., 2016; Zimmermann et al.,
738 2011), and species like *B. ephippiatus* can sustain gene flow and disperse in fragmented landscapes
739 (Landaverde-González et al., 2018), this resilience could diminish in the future. This decline in resilience
740 could, in part, be associated with climate change given that our analyses shows it to be a factor that
741 could potentially reduce the environmental suitability for bumble bees and reduce their climatic limits.
742 Such a change in adaptive/coping abilities would make bumble bees more sensitive to other threats
743 (Williams & Osborne, 2009) .

744 The creation of new, protected natural areas could benefit bumble bee species, especially in
745 mountainous regions such as the Trans-Mexican Volcanic Belt, which appears to be an important area
746 for several bumble bee species in terms of their CPD as well as their genetic patterns (Duennes et al.,
747 2017; Koch et al., 2018). However, this solution does not seem plausible since habitat fragmentation and
748 deforestation continues inside and outside these areas in the region studied and the remaining area of
749 natural land that could be put under protecting is diminishing (Harvey et al., 2008; Heino et al., 2015).
750 Furthermore, alarming evidence in a recent study showed a major loss of flying insect biomass even in
751 protected natural areas, that the authors suggested was associated with agricultural intensification in

752 the surrounding area (Hallmann et al., 2017). Together, these findings suggest that conservation efforts
753 should be redirected towards integrated landscape management strategies in which different land uses
754 and stakeholders (i.e. conservationists, local farmers) actively participate in restoring and managing the
755 landscape (Harvey et al., 2008). Special emphasis should be placed on restoring areas that were once
756 pine-oak forests habitats and tropical montane forests with open canopies, understory shrubs (Kappelle,
757 2006; Urbina-Cardona and Flores-Villela, 2010; Wesselingh et al., 2000), and promoting high-quality
758 habitats covered with native, flowering plants. These practices are key for bumble bees species due to
759 the fact that these bees correlate highly with these type of forests in Mesoamerica, and forage from
760 herbaceous native flowering plants and (Carvell et al., 2004; Hanula et al., 2015; Wesselingh et al.,
761 2000).

762 *4.3 Final considerations*

763 Ecological niche modelling can be used to understand species distributions and how these would change
764 under different climate change scenarios and models (Wiens et al., 2009). Nevertheless, there are
765 different caveats and problems that affect forecasts of species' CPDs and FPDs. These problems range
766 from sampling biases, RCPs and GCMs assumptions, algorithms chosen, model tuning, poor knowledge
767 of a species natural history, and changing characteristics of environmental conditions across space and
768 time (Peterson et al., 2018; Qiao et al., 2018). For this study, we tried to solve several of these biases
769 and errors; and believe our models should be further tested and refined in order to have better
770 predictions in the near future.

771 Other consideration to take into account are anthropogenic causes that could lead to wrong estimates
772 of species' CPDs based on niche models alone (Faurby and Araújo, 2018). As an example, we highlight
773 the species distribution model for *B. haueri*. This bumble bee species, based on our models, has the
774 second largest CPD of all the species. However, we know that most of its abundance and distributional
775 range has been reduced, particularly in northern Mexico and the Trans-Mexican Volcanic Belt because of
776 intense land-use change. This explains why this species was not seen for 24 years and is listed as
777 Endangered according to the Red List of Species of IUCN (Martínez-López and Pineda-Diez de Bonilla,
778 2015). We need to recognize that, although ecological niche modelling can help define a species'
779 potential distribution, there could be other reasons that explain the absence of a species in a predicted
780 area. Nevertheless, our models provide strong evidence that climate change will be an important threat
781 for bumble bee species in the future, and this finding should be considered for conservation efforts and
782 future Red List assessments.

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1033 Figure captions

1034 **Figure 1.** Map showing bumble bee sampling effort (values range from low to high in shades of grey to
1035 black) and the digital elevation model (elevation ranges from low in green to high in red) for
1036 Mesoamerica.

1037 **Figure 2.** Projections for climate change representative concentration pathways (RCPs) and global
1038 circulation models (GCMs) in 2050 (average 2041-2060) for three bumble bee species: a) RCP 4.5 for *B.*
1039 *steindachneri*, b) RCP 6.0 for *B. huntii*, c) RCP 8.5 for *B. ephippiatus*. The red areas represent current
1040 potential area lost, green areas future potential area gain, and yellow areas future potential stable
1041 areas. We chose three species as examples of species that can be found in low-lands (a), restricted to
1042 high mountains (b) and a common species found in middle range mountains in Mesoamerica (c). We
1043 chose three RCPs and GCMs to show the variability between models.

1044 **Figure 3.** Current and future (minimum and maximum) proportion of potential distributional area of
1045 bumble bee species within protected natural areas in Mesoamerica.

1046 **Figure 4.** Correlation analysis for 2050 (average 2041-2060) representative concentration pathways
1047 (RCPs) models mean and normalized current potential distribution (CPD) for bumble bee species in
1048 Mesoamerica. The x axis represents the normalized CPD. The y axis represents the change in the mean
1049 of the potential future distribution of each bumble bee species, the more negative the more climate
1050 change reduces the potential distribution of the species. The blue line represents the trend for all
1051 species ($r = 0.70$, $p < 0.01$). The red line represents the trend in which *B. pennsylvanicus* is not included ($r =$
1052 0.94 , $p < 0.01$).

1053 **Figure 5.** Habitat suitability change box-plot analysis for 2050 (average 2041-2060) representative
1054 concentration pathways models (RCPs). For each species, in the x axis the blue bar and box with lines
1055 represents the median, lower and upper quartile (25 to 75 percentile), and minimum and maximum
1056 values of habitat suitability change for the RCP 4.5 scenarios. The red and green bars represent the
1057 median of habitat suitability change for the RCP 6.0 and 8.5 scenarios. In the y axis the scale in which
1058 environmental suitability changes, from negative values (loss of environmental suitability) to positive
1059 values (gain in environmental suitability).

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1061 **Table 1. Range of current potential distribution (CPD) loss for bumble bee species in Mesoamerica for**
 1062 **the year 2050**

Species	CPD (ha)	RCP45	RCP60	RCP85	RCP45	RCP60	RCP85
		Min	Min	Min	Max	Max	Max
<i>B. brachycephalus</i>	34 197.887	40%	28%	41%	43%	40%	54%
<i>B. digressus</i>	1 956.530	10%	9%	9%	59%	76%	16%
<i>B. diligens</i>	41 235.609	19%	15%	15%	99%	20%	29%
<i>B. ephippiatus</i>	34 748.867	39%	26%	40%	49%	45%	53%
<i>B. haueri</i>	55 546.070	20%	13%	27%	98%	51%	49%
<i>B. huntii</i>	10 357.644	65%	64%	67%	100%	72%	89%
<i>B. macgregori</i>	3 992.945	47%	48%	52%	60%	67%	72%
<i>B. medius</i>	31 006.320	56%	52%	62%	84%	65%	73%
<i>B. mexicanus</i>	31 589.892	33%	27%	40%	56%	55%	57%
<i>B. nigrodorsalis</i>	14 172.806	58%	51%	65%	95%	80%	85%
<i>B. pennsylvanicus</i>	125 530.939	20%	17%	25%	69%	35%	31%
<i>B. pullatus</i>	18 459.771	39%	35%	48%	46%	52%	56%
<i>B. steindachneri</i>	42 737.116	8%	7%	11%	93%	24%	33%
<i>B. trinominatus</i>	2 614.399	50%	30%	55%	68%	72%	72%
<i>B. variabilis</i>	38 172.030	57%	49%	60%	72%	72%	72%
<i>B. weisi</i>	21 057.829	37%	29%	41%	54%	52%	57%
<i>B. wilmattae</i>	11 896.828	18%	17%	20%	45%	41%	56%
<i>B. xelajuensis</i>	561.298	34%	30%	46%	100%	67%	62%

1063 **Table 1.** Range of loss of bumble bee species' current potential distribution in Mesoamerica for the year
 1064 2050 (average for 2041-2060). The percentage of loss is presented as the minimum and maximum
 1065 obtained in each of the three RCP models. The color gradient depicts loss intensity (from low in yellow to
 1066 high in red).

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1068 **Table 2. Range of current potential distribution (CPD) loss for bumble bee species in Mesoamerica for**
 1069 **the year 2070**

Species	CPD	RCP45	RCP60	RCP85	RCP45	RCP60	RCP85
		Min	Min	Min	Max	Max	Max
<i>B. brachycephalus</i>	34 197.887	42%	44%	49%	54%	57%	72%
<i>B. digressus</i>	1 956.530	14%	8%	9%	55%	82%	61%
<i>B. diligens</i>	41 235.609	24%	19%	32%	26%	26%	50%
<i>B. ephippiatus</i>	34 748.867	45%	42%	65%	46%	51%	75%
<i>B. haueri</i>	55 546.070	26%	26%	47%	55%	62%	59%
<i>B. huntii</i>	10 357.644	75%	75%	86%	85%	89%	94%
<i>B. macgregori</i>	3 992.945	66%	59%	72%	70%	73%	88%
<i>B. medius</i>	31 006.320	61%	60%	73%	70%	74%	83%
<i>B. mexicanus</i>	31 589.892	40%	40%	53%	48%	57%	78%
<i>B. nigrodorsalis</i>	14 172.806	65%	66%	86%	82%	87%	95%
<i>B. pensylvanicus</i>	125 530.939	22%	24%	32%	38%	46%	44%
<i>B. pullatus</i>	18 459.771	44%	47%	60%	50%	58%	77%
<i>B. steindachneri</i>	42 737.116	9%	8%	19%	16%	27%	29%
<i>B. trinominatus</i>	2 614.399	56%	55%	75%	64%	71%	88%
<i>B. variabilis</i>	38 172.030	62%	63%	70%	64%	75%	85%
<i>B. weisi</i>	21 057.829	45%	42%	64%	52%	61%	82%
<i>B. wilmattae</i>	11 896 828	23%	23%	40%	49%	59%	65%
<i>B. xelajuensis</i>	561 298	38%	42%	67%	70%	69%	96%

1070 **Table 2.** Range of loss of bumble bee species' current potential distribution in Mesoamerica for the year
 1071 2070 (average for 2061-2080). The percentage of loss is presented as the minimum and maximum
 1072 obtained in each of the three RCP models. The color gradient depicts loss intensity (from low in yellow to
 1073 high in red).

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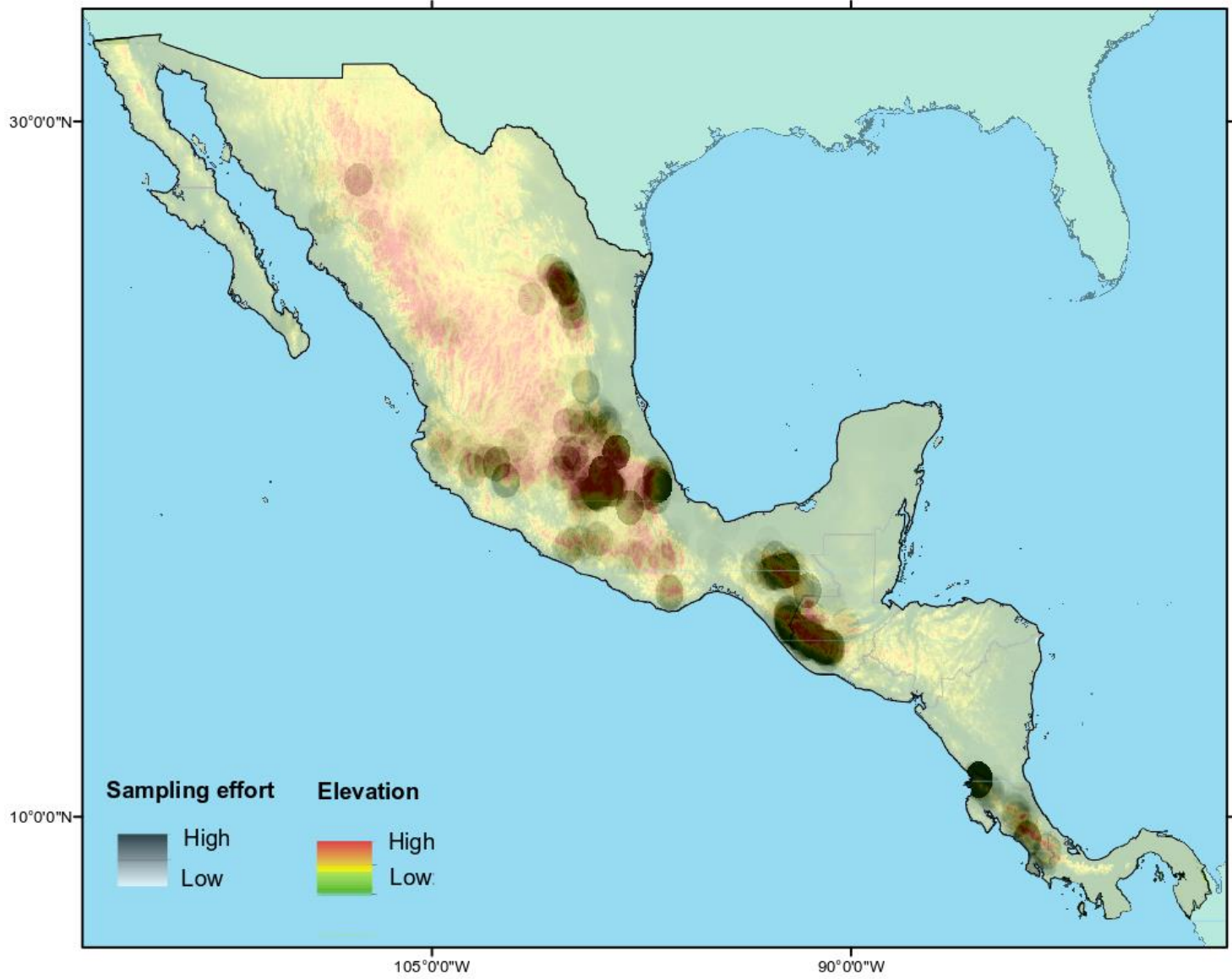


Fig. 1. Sampling effort and area of study

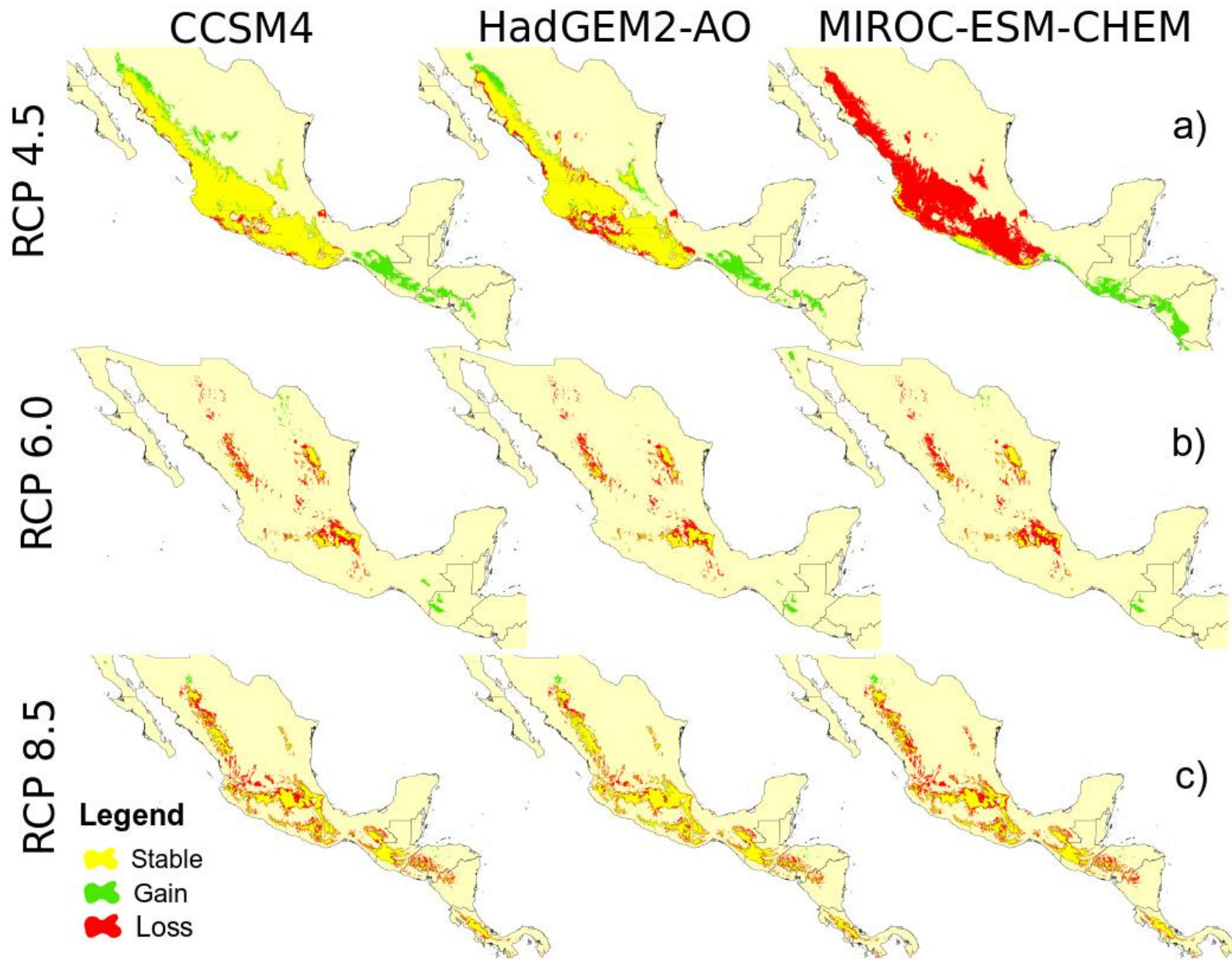


Fig. 2. Climate change representative concentration pathways models for 2050 (average 2041-2060)

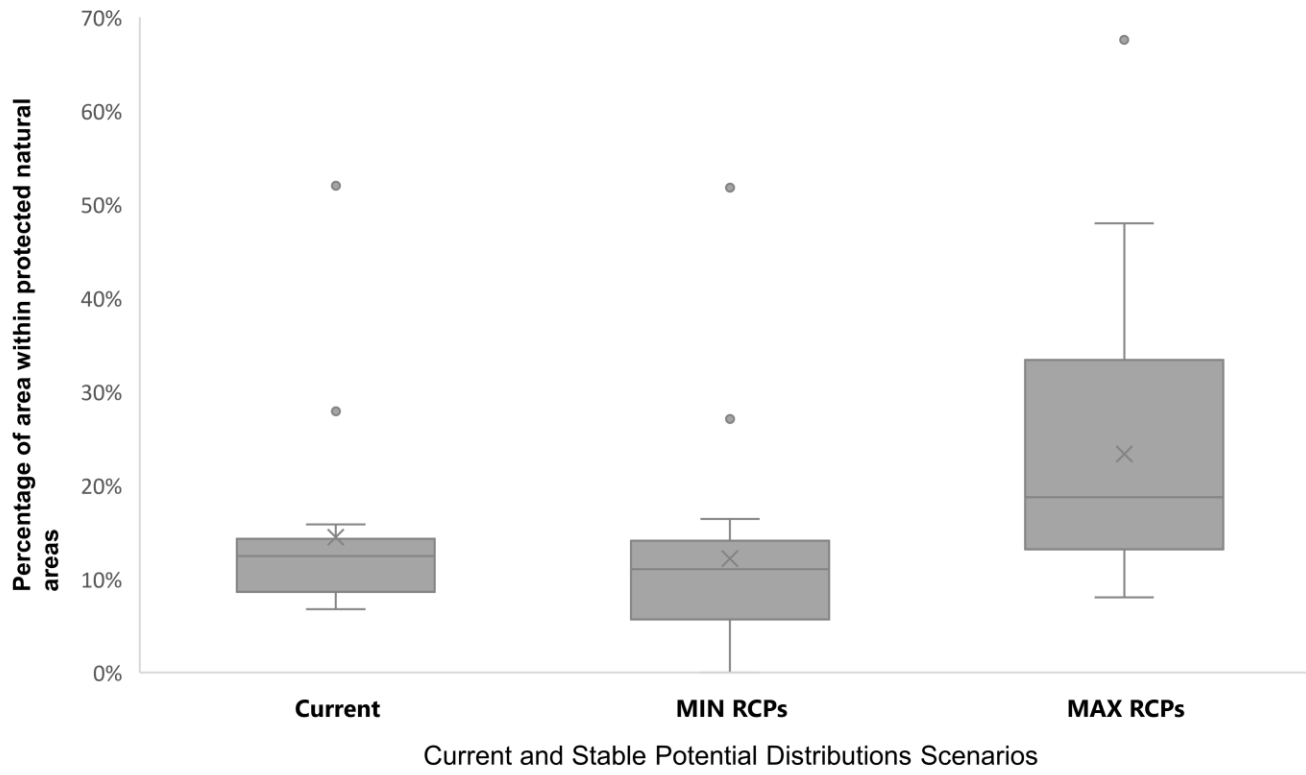


Fig. 3. Range of potential distribution area within protected natural areas for bumble bee species in Mesoamerica

2050-RCP Models-Mean and Normalized Current Potential Distribution

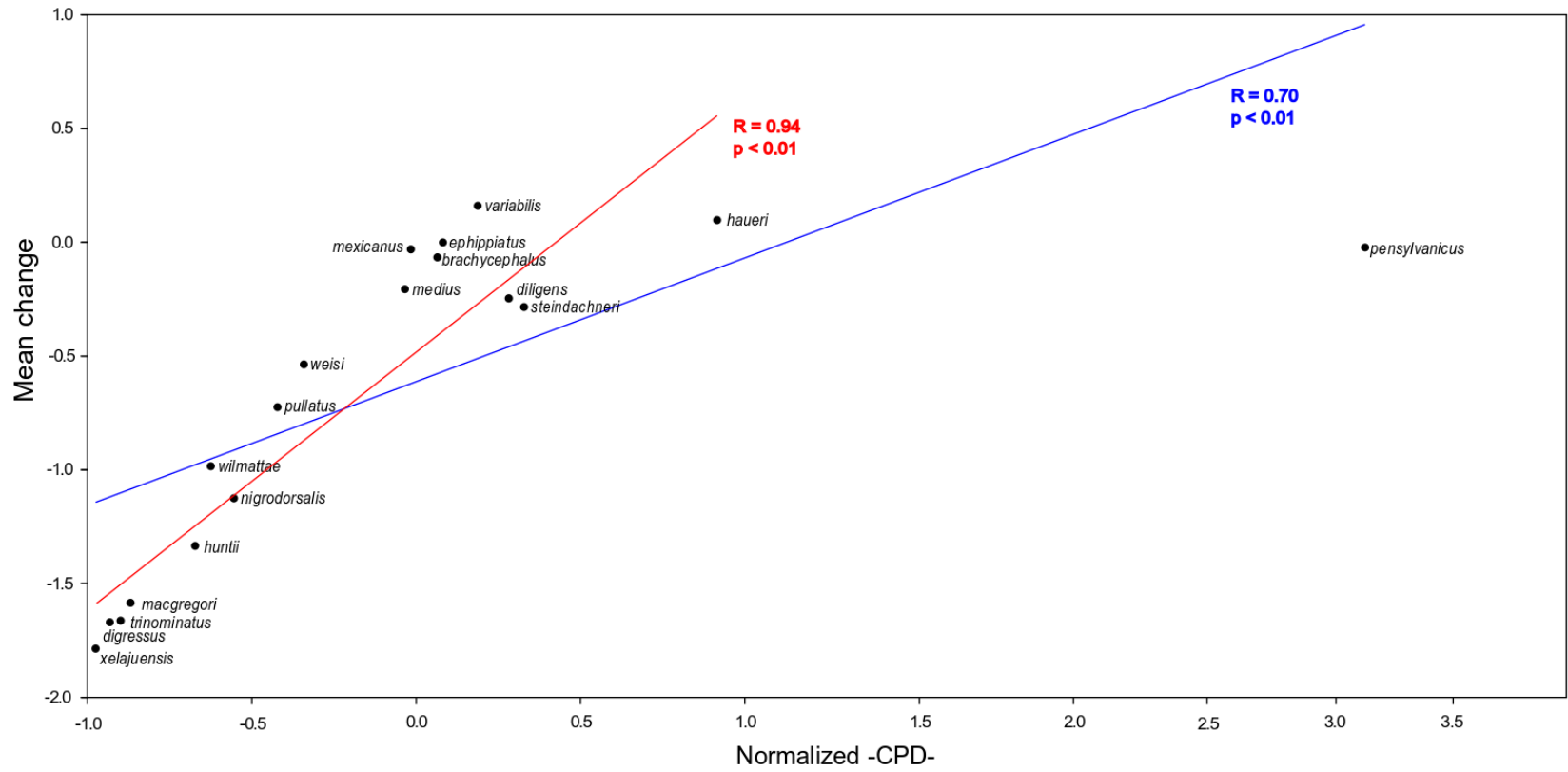


Fig. 4. Correlation analysis of normalized current potential distribution with mean change for the year 2050 (average 2041-2060)

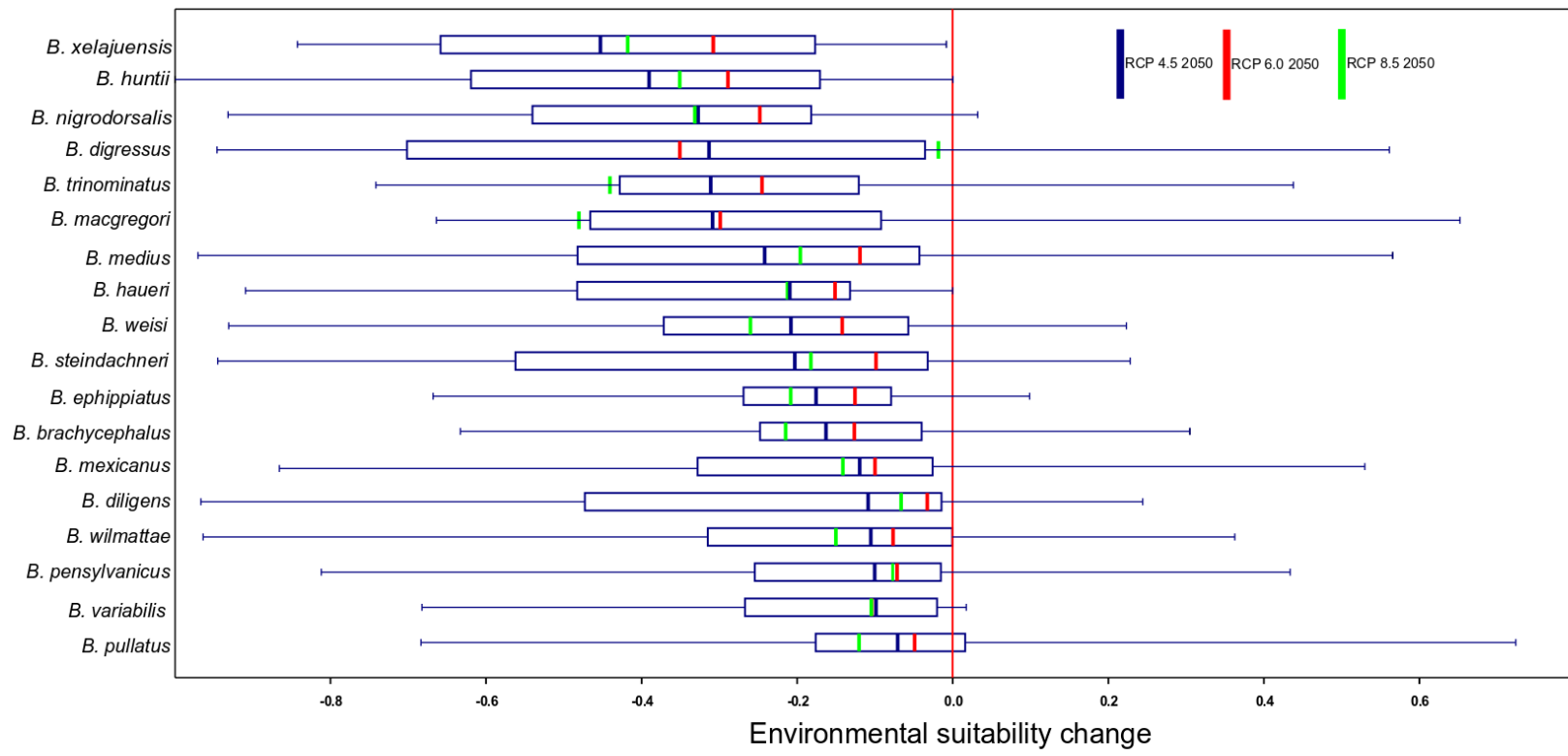


Fig. 5. Median values for environmental suitability change in bumble bee species for the year 2050 (average 2041-2060)

Supplementary material

Table A1. Bioclimatic variables from Worldclim

Variable	Interpretation
Bio 1	Annual mean temperature
Bio 2	Mean diurnal range
Bio 3	Isothermality
Bio 4	Temperature seasonality
Bio 5	Maximum temperature of warmest month
Bio 6	Minimum temperature of coldest month
Bio 7	Temperature annual range
Bio 8	Mean temperature of wettest quarter
Bio 9	Mean temperature of driest quarter
Bio 10	Mean temperature of warmest quarter
Bio 11	Mean temperature of coldest quarter
Bio 12	Annual precipitation
Bio 13	Precipitation of wettest month
Bio 14	Precipitation of driest month
Bio 15	Precipitation seasonality (coefficient of variation)
Bio 16	Precipitation of wettest quarter
Bio 17	Precipitation of driest quarter
Bio 18	Precipitation of warmest quarter
Bio 19	Precipitation of coldest quarter

Table A1. Bioclimatic variables from Worldclim version 1 (Hijmans, et al., 2005) at 30 arc seconds used to generate current and future potential distribution of bumble bees from Mesoamerica. Temperature variables are measured in Celsius degrees °C and precipitation in mm. Unitless variables are isothermality, temperature seasonality and precipitation seasonality.

Table A2. Species modeled in this study with the chosen threshold and settings for Maxent

Species	Equal sensitivity and	Settings for Maxent		Variables chosen for	AUC
	specificity area	Features	Regularization multiplier	models	
<i>B. brachycephalus</i>	0.216	LQ	1	2, 4, 9, 15, 16, 18	0.790
<i>B. digressus</i>	0.06	L	1	3, 4, 7, 12, 18	0.944
<i>B. diligens</i>	0.275	LQHP	3	3, 4, 6, 12, 18	0.792
<i>B. ephippiatus</i>	0.158	LQHP	1	3, 4, 10, 12, 15, 18	0.914
<i>B. haueri</i>	0.237	L	2	3, 7, 11, 12, 14, 19	0.831
<i>B. huntii</i>	0.06	LQHP	2.5	3, 6, 7, 15, 16, 19	0.980
<i>B. macgregori</i>	0.076	LQ	1.5	4, 5, 13, 15, 19	0.968
<i>B. medius</i>	0.186	LQHP	2	1, 3, 4, 7, 14	0.892
<i>B. mexicanus</i>	0.242	LQHP	3.5	2, 3, 6, 12, 15	0.838
<i>B. nigrodorsalis</i>	0.088	LQH	2.5	1, 4, 8, 12, 17	0.965
<i>B. pensylvanicus</i>	0.236	LQHP	1	1, 3, 7, 9, 13, 15	0.845
<i>B. pullatus</i>	0.153	LQHP	3	3, 6, 15, 19	0.900
<i>B. steindachneri</i>	0.193	LQHP	2	3, 6, 15, 16, 17	0.868
<i>B. trinominatus</i>	0.033	LQH	3	4, 8, 13, 18	0.981
<i>B. variabilis</i>	0.164	LQHP	1	2, 3, 5, 7, 9, 14	0.913
<i>B. weisi</i>	0.128	LQHP	1	4, 10, 12, 15, 19	0.941
<i>B. wilmattae</i>	0.196	LQ	1	3, 4, 14, 18	0.850
<i>B. xelajuensis</i>	0.098	LQH	1	4, 6, 14, 18	0.921

Table A1. Species, values, and variables used to estimate the current and future potential distribution of bumble bees from Mesoamerica. Features (L = Linear, Q = Quadratic, H = Hinge, P = Product), and regularization multiplier were obtained in the Wallace package by selecting the optima model based on Akaike's Information Criterion (AICc) values. The variables chosen for the final models were selected by visually evaluating the response curves for each bumble bee species. We also present the AUC values for model evaluation.

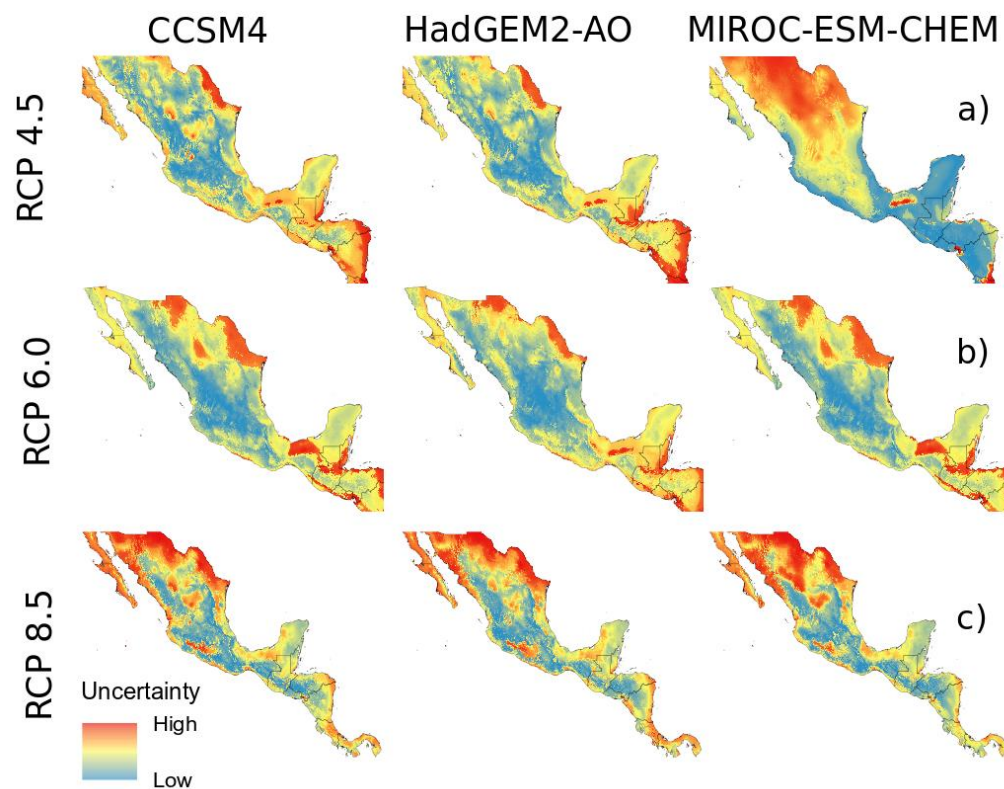


Fig. A.1. Multivariate Environmental Similarity Surface (MESS) analyses for climate change representative concentration pathways models for 2050 (average 2041-2060)

Figure A.1. Multivariate Environmental Similarity Surface (MESS) analyses for climate change projections presented in fig. 2 of the manuscript for three bumble bee species: a) RCP 4.5 for *B. steindachneri*, b) RCP 6.0 for *B. huntii*, c) RCP 8.5 for *B. ephippiatus*. The red areas represent high uncertainty in the projections outside the calibration area while blue areas represent low uncertainty in the projections outside the calibration area. We chose three species as examples of species that can be found in low-lands (a), restricted to high mountains (b) and a common species found in middle range mountains in Mesoamerica (c). We chose three RCPs and GCMs to show the variability between models.

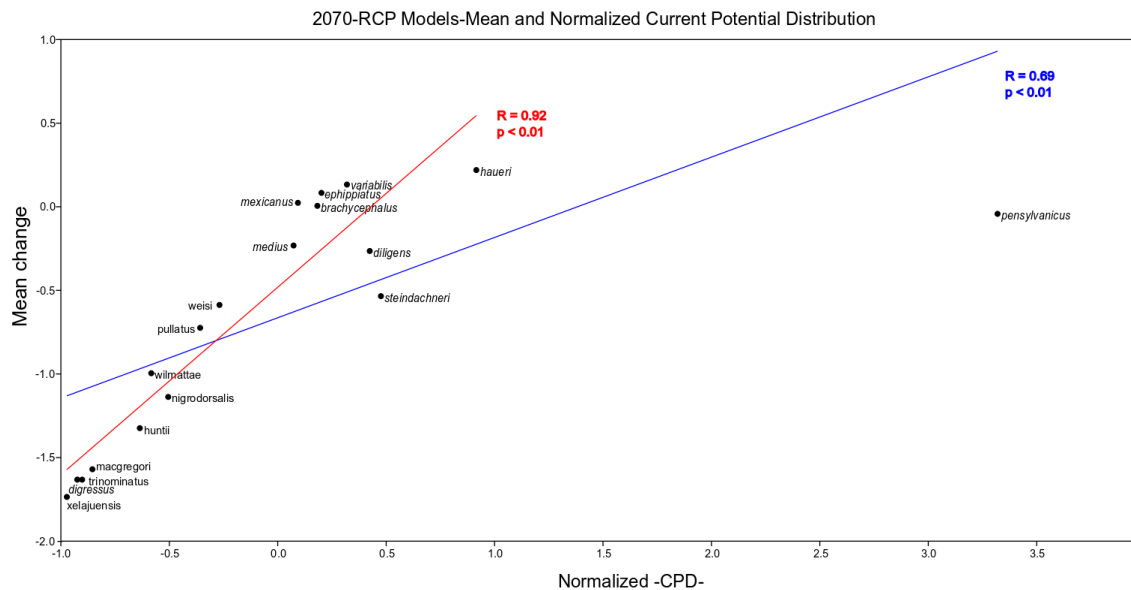


Fig. A.2. Correlation analysis of normalized current potential distribution with mean change for the year 2070 (average 2061-2080)

Fig. A.2. Correlation analysis for 2070 (average 2061-2080) representative concentration pathways (RCPs) models mean and normalized current potential distribution (CPD) for bumble bee species in Mesoamerica. The x axis represents the normalized CPD. The y axis represents the change in the mean of the potential future distribution of each bumble bee species, the more negative the more climate change reduces the potential distribution of the species. The blue line represents the trend for all species ($r = 0.69$, $p < 0.01$). The red line represents the trend in which *B. pensylvanicus* is not included ($r = 0.92$, $p < 0.01$).

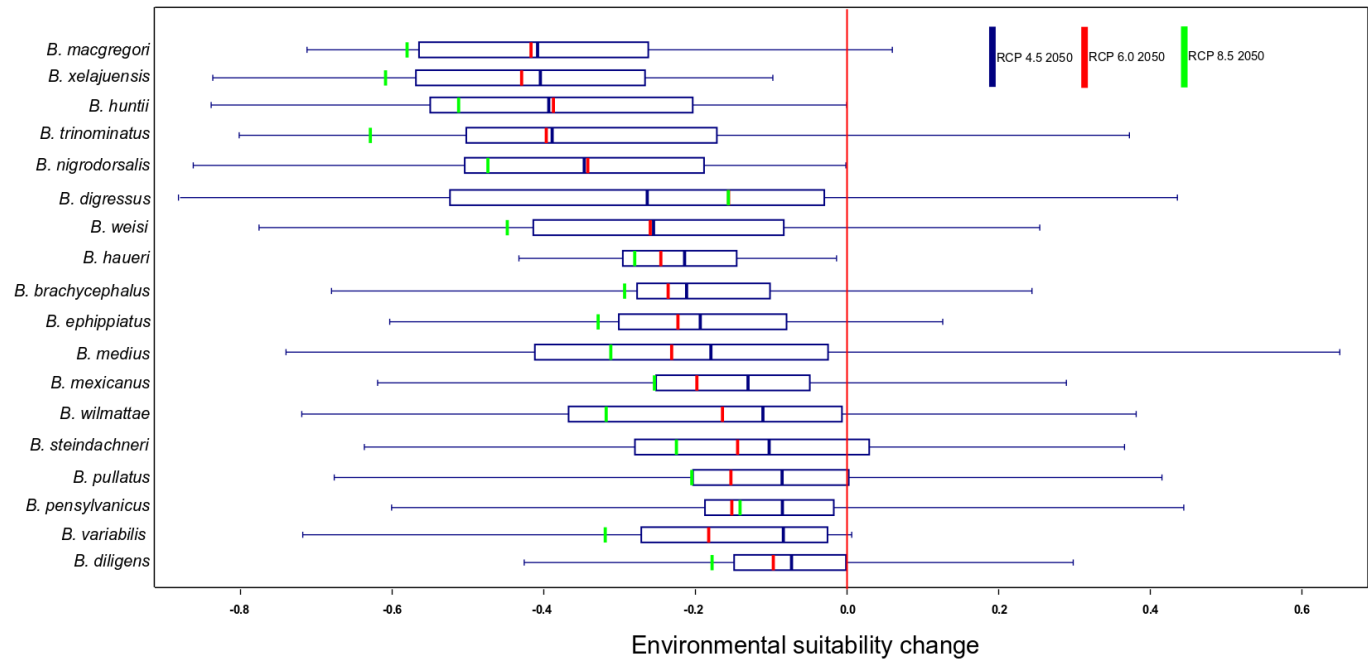


Fig. A.3. Median values for environmental suitability change in bumble bee species for the year 2060 (average 2061-2080)

Fig.A.3. Habitat suitability change box-plot analysis for 2070 (average 2061-2080) representative concentration pathways models (RCPs). For each species, in the x axis the blue bar and box with lines represents the median, lower and upper quartile (25 to 75 percentile), and minimum and maximum values of habitat suitability change for the RCP 4.5 scenarios. The red and green bars represent the median of habitat suitability change for the RCP 6.0 and 8.5 scenarios. In the y axis the scale in which environmental suitability changes, from negative values (loss of environmental suitability) to positive values (gain in environmental suitability).

Capítulo 3

Conclusiones

Basado en los análisis de modelado de nicho ecológico para el cálculo de la distribución potencial actual y futura de los abejorros de Mesoamérica, encontré que habrá reducciones en la distribución potencial futura de las 18 especies de abejorros de la región a causa del cambio climático. Un factor relacionado con el cálculo de la reducción de la distribución potencial futura es que los resultados de todos los modelos varían en el porcentaje de predicción. El modelo MIROC-ESM-CHEM para el año 2050 Y 2070 resultó ser el más severo en el pronóstico de la reducción de la distribución potencial futura para muchas especies de *Bombus* (**Anexo 1 y 2**). En un estudio realizado por Guevara, Morrone y León-Paniagua (2018) estos encontraron que el modelo MIROC para el cálculo de distribución de varias especies fue más dramático para el último glaciario máximo, lo cual estaba relacionado con las propiedades intrínsecas del modelo y los diferentes supuestos que tienen los modelos (Guevara et al. 2018).

Todos los modelos utilizados en el presente estudio pronostican una reducción en la distribución potencial futura de todas las especies de abejorros de la región. Basado en el análisis de correlación, esta reducción afectará de una mayor manera a las especies raras con áreas de distribución restringida, en comparación con especies generalistas con amplia distribución. Esto también estará acompañado en una reducción de la idoneidad ambiental. Esta evidencia se suma a la encontrada para abejas y abejorros de otras regiones del planeta (Giannini et al. 2012; Kerr et al. 2015; Martins et al. 2015; Rasmont et al. 2015; IPBES 2016; Sirois-Delisle and Kerr 2018).

La reducción de distribución potencial futura en los límites de la distribución geográfica para los abejorros de Mesoamérica y la persistencia de área cercana al centro de su distribución, encontrada en el presente estudio, se suma a la evidencia encontrada a favor de este fenómeno en otros estudios para abejas y abejorros (Giannini et al. 2012; Martins et al. 2015). La hipótesis que la pérdida en el rango geográfico de las especies es mayor en los límites de su distribución en comparación a su centroide tiene evidencia empírica que la soporta, sin embargo, este debate aún continua (Martínez-Meyer et al. 2013; Osorio-Olvera et al. 2016; Lee-Yaw et al. 2017; Soberón et al. 2018). A pesar de que la evidencia que encontré solo la exploré en el espacio geográfico, es importante comprobar esta hipótesis en el espacio ambiental que, junto a estudios demográficos permitirían entender los mecanismos que generan este patrón.

Mis resultados estimaron para todas las especies áreas potenciales futuras que podrían ser idóneas para los abejorros de esta región y que en la actualidad no lo son. No tomé en cuenta para mis cálculos estas áreas, ya que necesitamos más información sobre los patrones de dispersión de las especies de abejorros en Mesoamérica. Esto nos permitiría considerar, a partir de patrones de dispersión, si estas nuevas áreas podrían ser accesibles o no para las especies de la región. Este estudio podría ser la base para realizar más análisis, una vez entendidos los mecanismos que generan estos patrones. Sin embargo, es importante mencionar que un estudio reciente para abejorros de Canadá y Estados Unidos de América tomo en cuenta las habilidades de dispersión de las especies de abejorros y las proyecciones hacia el futuro no mejoraban (Sirois-Delisle and Kerr 2018).

Las áreas naturales protegidas actúan como unidades fundamentales para la conservación (Chape et al. 2005), éstas podrían ayudar a proteger porciones de la distribución potencial futura de las especies de abejorros en Mesoamérica (Martins et al. 2015). Sin embargo, las áreas naturales protegidas históricamente no fueron creadas para la protección de la biodiversidad, sino para otros usos (i.e. belleza escénica, paisajes poco productivos) a excepción de las reservas de la biosfera (Pressey et al. 2002; Halfter 2011; Monteiro et al. 2018). En este estudio corroboramos que las áreas naturales protegidas cubren una pequeña parte de la distribución potencial actual de las especies de abejorros de la región. Una excepción es para el abejorro *B. digressus*, el cual se distribuye en Costa Rica y el cual en la actualidad más de la mitad de su distribución potencial actual se encuentra dentro de áreas naturales protegidas.

El incremento del porcentaje de cobertura de las áreas naturales protegidas en la distribución potencial futura, en comparación con la distribución potencial actual, de las especies de abejorros de Mesoamérica se da por una fuerte disminución del área potencial futura de estas especies fuera de las áreas naturales protegidas. Esto significa que lo que queda de la distribución potencial futura empata en mayor medida con las áreas naturales protegidas. Sin embargo, estos datos no son alentadores, ya que para comenzar el porcentaje de cobertura de la distribución potencial actual dentro áreas naturales protegidas es muy bajo. Incluso, la presión que existe en las áreas naturales protegidas como deforestación causará que éstas áreas se reduzcan, lo que afectará a los abejorros indirectamente.

Por lo tanto, considero que aumentar el número de áreas naturales protegidas en ciertos tipos de hábitat asociados a estas especies de abejorros podrá ayudar a la conservación de estos polinizadores. Usualmente estas especies se distribuyen en montañas con características de bosques templados y/o vegetación alpina, pero algunas especies se distribuyen en tierras bajas tropicales y bosques lluviosos. Por lo tanto, las regiones que se podrían beneficiar de la creación de áreas naturales protegidas serían las montañas del eje Neovolcánico Transversal Mexicano ya que muchas especies de abejorros empatan sus distribuciones en esta región. Otras regiones que se podrían beneficiar serían las montañas de Guerrero y Oaxaca, así como el altiplano guatemalteco. Estas áreas deben de contener hábitats con bosques de pino-encino como lo proponen Urbina-Cardona y Flores-Villela (2010). Esta no es la única solución, es fundamental que se tomen en cuenta las distintas dinámicas que caracterizan los distintos paisajes de México y Centro América. Cada contexto y región tiene sus propias fortalezas, amenazas, oportunidades y debilidades, las cuales deben de ser tomadas en cuenta para implementar planes de conservación y mitigación para polinizadores y abejorros frente al cambio climático.

Para finalizar, es importante entender que el modelaje de nicho ecológico tiene sus fortalezas y debilidades. Es una herramienta útil que puede ser multifuncional, tanto para incrementar el entendimiento de la distribución de las especies (Pearson et al. 2007; Cardoso et al. 2011) como para acompañar planes de conservación e identificación de áreas prioritarias para la conservación, creación de nuevas áreas naturales protegidas, probar hipótesis de conservadurismo de nicho, taxonomía, invasión potencial de

especies y cambio climático (Baldwin 2009; Anacker et al. 2010; Escobar et al. 2014; Prieto-Torres et al. 2018; Sirois-Delisle and Kerr 2018). Sin embargo, el conocimiento de las especies a modelar debe de ir acompañado de buenas prácticas en cuanto al manejo de la teoría de nicho ecológico, los diferentes algoritmos que existen, la pregunta de investigación, los ajustes que se deben de realizar a los algoritmos, información georreferenciada correctamente, relación entre especies y variables ambientales, visualización de modelos y cuidado en las interpretaciones de las áreas de distribución potencial que se obtienen (tanto en el presente como en proyecciones de invasiones y cambio climático) y cálculos de esfuerzo de muestreo para tener una certitud de nuestros modelos.

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Anexos

Anexo 1. Modelos que predicen una mayor pérdida de distribución potencial futura para los abejorros de Mesoamérica para el año 2050

Especies	Escenarios		
	RCP4.5	RCP6.0	RCP8.5
<i>B. brachycephalus</i>	CCSM4	CCSM4	MIROC-ESM-CHEM
<i>B. digressus</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	CCSM4
<i>B. diligens</i>	MIROC-ESM-CHEM	CCSM4	CCSM4/MIROC-ESC-CHEM
<i>B. ephippiatus</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. haueri</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. huntii</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. intrudens</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. macgregori</i>	HADGEM2-AO	MIROC-ESM-CHEM	CCSM4/ HADGEM2-AO
<i>B. medius</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. mexicanus</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. nigrodorsalis</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. pensylvanicus</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. pullatus</i>	HADGEM2-AO	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. steindachneri</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. trinominatus</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. weisi</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. wilmattae</i>	CCSM4	CCSM4	CCSM4
<i>B. xelajuensis</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM

Anexo 2. Modelos que predicen una mayor pérdida de distribución potencial futura para los abejorros de Mesoamérica para el año 2070

Especies	Escenarios		
	RCP4.5	RCP6.0	RCP8.5
<i>B. brachycephalus</i>	CCSM4	CCSM4	CCSM4
<i>B. digressus</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	CCSM4
<i>B. diligens</i>	CCSM4	CCSM4	MIROC-ESC-CHEM
<i>B. ephippiatus</i>	HADGEM2-AO	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. haueri</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. huntii</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. intrudens</i>	CCSM4/MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. macgregori</i>	CCSM4	CCSM4	CCSM4
<i>B. medius</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. mexicanus</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. nigrodorsalis</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. pensylvanicus</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. pullatus</i>	HADGEM2-AO	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. steindachneri</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. trinominatus</i>	MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. weisi</i>	HADGEM2-AO/MIROC-ESM-CHEM	MIROC-ESM-CHEM	MIROC-ESM-CHEM
<i>B. wilmattae</i>	CCSM4/HADGEM2-AO	CCSM4	CCSM4/HADGEM2-AO
<i>B. xelajuensis</i>	HADGEM2-AO	MIROC-ESM-CHEM	MIROC-ESM-CHEM